Quantifying niche availability, niche overlap and competition for recruitment sites in plant populations without explicit knowledge of niche axes.

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ABSTRACT

1. Niche availability, niche overlap and competitive ability are key determinants of the distribution and abundance of species. However, quantifying each of these components is difficult because it is not always possible to identify or measure relevant environmental gradients (niche axes) along which species might partition or compete for niche space.

2. We describe a method that uses seed addition experiments to quantify the number of 'safe-sites' (microsites suitable for a species to recruit from seed) at a location and show how

this method can be used to quantify niche availability, niche overlap and competitive ability. We illustrate our approach using two seed addition experiments in grassland.

3. In the first experiment, we added seeds of one native and two exotic grass species, alone and in mixture, to plots that were arrayed along a gradient of soil moisture availability. We show that the three species partitioned safe-sites, implying that all three species could locally co-occur through niche partitioning, in part due to different responses to moisture availability.

4. In the second experiment, we added seeds of three commonly co-occurring native grass species, alone and in mixture, to plots with no obvious environmental gradients. One species outcompeted two others for site occupancy, allowing us to quantify both the degree of niche overlap and the relative ability of each species to compete for safe-site occupancy without *a priori* knowledge of the niche axes. Results from both experiments demonstrate the fine-scales at which species can partition niches to facilitate co-occurrence.

5. *Synthesis.* By conceptualising a plot of ground as containing a limited number of microsites that are safe for the recruitment of a given species, and using seed addition experiments to measure both the number of safe-sites and degree of safe-site overlap among species, we show how niche availability, niche overlap and competitive ability can be quantified at fine-scales without *a priori* knowledge of niche axes. Our approach allows questions about niche availability and competition for shared niche space to be empirically tested, and to examine how these processes vary along environmental gradients to shape species distributions and patterns of co-occurrence.

Keywords: biotic interactions, coexistence, competition, environmental heterogeneity, facilitation, grasslands, niche partitioning, recruitment function, seed limitation, fundamental niche.

INTRODUCTION

The distribution and local abundance of plant species is determined, in part, by the match between species' requirements for recruitment and local environmental conditions. However, where species have similar requirements for recruitment, such that their fundamental niches overlap, competition among species may exclude some from sites they could otherwise occupy (Esch, Ashbacher, Kopp, & Cleland, 2018; Levine & HilleRisLambers, 2009; MacArthur & Levins, 1967). Consequently, if a species is not seed or dispersal limited, its distribution and abundance should depend on: 1) the availability of fundamental niche space (niche availability); 2) the degree to which species' fundamental niches overlap (niche overlap); and 3) the ability of species to compete with other species for overlapping niche space (competitive ability). The potential for species to co-occur at a location depends on the interplay among these components. Species could co-occur if they partition niche space, or if each species has a competitive advantage over other species in at least some portion of shared niche space (Gause, 1934; MacArthur & Levins, 1964). While these concepts are fundamental to understanding how plant communities are structured, it has proven difficult to devise methods that allow us to simultaneously measure niche availability, niche overlap and competitive ability in the field.

Current approaches to assess the degree to which species partition or compete for niche space, and how this influences co-occurrence, stem from co-existence models (Letten, Ke, & Fukami, 2016). Two main approaches are recognised. First, models of interacting species can be used to quantify the relative strength of intra- to inter-specific density dependence and resulting niche and fitness differences, which then determine whether two species can coexist (modern coexistence theory; Chesson, 2000). Second, mechanistic consumer-resource models (contemporary niche theory; Chase & Leibold, 2003) aim to quantify how species use particular resources, and how differences in resource use then influence the potential to coexist

(MacArthur & Levins, 1964; Tilman, 1982). However, neither approach provides a straightforward way to quantify niche availability, which is necessary to understand first how local environmental conditions determine where individual plant species could potentially occur, and subsequently how interactions among plant species determine realised patterns of distribution and abundance. Specifically, modern coexistence theory identifies only niche differences, which are defined in terms of the relative strength of interactions among and within species, while in consumer-resource models niches are defined in terms of specific limiting resources, which may not always be obvious.

A key difficulty with measuring both niche availability for single species and niche partitioning among species is that the measurements often rely on identifying the relevant axes along which species might differ in their niche requirements (Silvertown & Law, 1987; Tilman, 1982). While there is strong evidence that niche partitioning along environmental gradients allows species to co-occur (García-Baquero, Silvertown, Gowing, & Valle, 2016; Pickett & Bazzaz, 1978; Rees, 2013; Tilman, 1987), co-occurring species often also show substantial niche overlap (Berdugo et al., 2018; Mahdi, Law, & Willis, 1989). Species with niches that appear to overlap along a specific gradient may co-occur because one or both species is dispersal limited (Soberon, 2007), but might also co-occur because they partition niches along other, unidentified niches axes (Silvertown, 2004). The difficulty in identifying relevant axes along which species might partition niches is exacerbated by the very fine spatial scale at which plant species can respond to environmental variation (Harper, Williams, & Sagar, 1965; Stowe & Wade, 1979). For example, up to 89 species have been recorded within 1 m^2 of temperate grassland (Cantero, Partel, & Zobel, 1999), but it is difficult to measure environmental variation, and thus quantify niche availability and niche differentiation, at such fine-scales (Blonder et al., 2018; Snaydon, 1962).

Our aim in this paper is to overcome some of the difficulties in measuring niche availability, niche overlap and competitive ability by describing a relatively straightforward way to quantify each component in the field without knowing the specific axes along which niches may vary. We do this by conceptualising a plot of ground as comprising an array of microsites, each large enough to support a single plant (c.f. the regeneration niche of Grubb, 1977). Species-specific requirements for germination and seedling establishment mean that even small differences among microsites can alter conditions to favour the recruitment of one species over another (Fowler & Antonovics, 1981; Harper et al., 1965). Because the number of microsites suitable for a given species will vary among habitats and along environmental gradients (Duncan, Diez, Sullivan, Wangen, & Miller, 2009; Miller et al., 2014; Spotswood, Mariotte, Farrer, Nichols, & Suding, 2016), locations with greater numbers of microsites suitable for a given species coincide with areas of greater fundamental niche availability. Measuring the number of suitable microsites at different locations thus allows us to quantify niche availability without knowing precisely what underpins recruitment outcomes. By extension, species with similar requirements for germination and growth will share microsites suitable for recruitment (Aicher, Larios, & Suding, 2011). Consequently, the degree to which two species share suitable microsites reflects their degree of niche overlap, while the ability of one species to occupy shared microsites at the expense of a second species reflects their relative competitive abilities.

Using this approach, we outline a model that can be parameterised with data from seed addition experiments to simultaneously quantify: 1) the availability of microsites that are suitable for recruitment (i.e. "safe" sensu Harper, Clatworthy, McNaughton, & Sagar, 1961) as a proxy for niche availability; 2) the degree to which microsites that are suitable for one species are shared by another (niche overlap); and 3) relative competitive ability when species compete for occupancy of shared microsites (competitive ability). We use data from two grassland

experiments to illustrate this approach, highlighting the potential for fine-scale niche differentiation to allow multiple species to co-occur in plant communities.

MATERIALS AND METHODS

Conceptual model

Our model builds on the approach outlined in Duncan et al. (2009), which uses data from seed addition experiments to estimate the availability of microsites suitable for the recruitment of a single species. We first describe the single species model and how it can be used to estimate niche availability for a given species; we then introduce an extension that estimates niche overlap among species, and species' relative competitive abilities for shared niche space.

Quantifying niche availability

The underlying single-species recruitment model conceptualises a plot of ground as comprising an array of n_i microsites. Each microsite is an area large enough to supply the resources needed to support a single individual of species *i*. Values of n_i could vary among species if some require a larger or smaller area to support a single individual and, for a given species, could vary through time if a larger area is required to support individuals as they increase in size (Duncan et al., 2009). Of n_i microsites that could support a single individual of species *i*, only a proportion, b_i, have conditions suitable for successful recruitment of that species. From here on we refer to microsites that are suitable for the recruitment of a species as "safe-sites" (sensu Harper et al., 1961).

Given n_i and b_i, two processes determine the number of individuals, r_i, that recruit given the arrival of s_i seeds. First, seeds landing in unsafe-sites will fail to recruit because they encounter conditions unsuitable for germination or survival. Failure to recruit due to landing in an unsafe-site is a density-independent process: each arriving seed has probability 1 - b_i of failing to land

in a safe-site regardless of the number of arriving seeds. Second, because safe-sites can support only one individual, seeds of species *i* landing in the same safe-site must compete for safe-site occupancy, with only a single individual recruiting regardless of how many seeds arrive. This is a density-dependent process: with greater numbers of arriving seeds, more seeds will fail to recruit due to competition for safe-site occupancy.

If seeds are randomly dispersed in a plot, such that each seed has the same probability of landing in any microsite (given that the experimenter controls the distribution of seeds across plots; for an alternative see Brannstrom & Sumpter, 2005), the expected number of individuals recruiting from s_i seeds is (see Duncan et al., 2009):

$$r_i = b_i n_i \left(1 - e^{s_i / n_i}\right) \qquad \text{Equation 1}$$

Parameters b_i and n_i can be estimated by fitting Equation 1 to data from a seed addition experiment where different numbers of seeds are added to different plots and the resulting number of recruits are recorded. Equation 1 describes a recruitment curve with an asymptote at $b_i n_i$, which is the total number of safe-sites per plot and hence the number of individuals that would recruit if seeds landed in all safe-sites (i.e., the plot was saturated with seeds) (Aicher et al., 2011; Duncan et al., 2009; Miller et al., 2014; Spotswood et al., 2016).

The parameters b_i and $b_i n_i$ both measure fundamental niche availability. Parameter b_i is the proportion of a plot comprising safe-sites, which equates to the area of fundamental niche space available, while $b_i n_i$ is the total number of safe-sites, with a greater number of safe-sites implying more available niche space.

Quantifying niche overlap and competitive ability

Current recruitment models (Duncan et al., 2009; Spotswood et al., 2016) do not consider how competition between species can affect recruitment, which would occur if two or more species have overlapping niches and compete for occupancy of the same safe-sites.

For two species, *i* and *j*, we can estimate the degree to which their niches overlap and they compete for safe-site occupancy by: 1) experimentally adding seeds of each species to plots of a given size in monoculture, and obtaining species-specific estimates of niche availability (e.g., $b_i n_i$ and $b_j n_j$; Fig. 1a, b); and 2) adding seeds of both species to a single plot at seed densities high enough to saturate safe-sites, such that seeds of each species must compete for occupancy of any shared safe-sites, and recording the numbers of each species that recruit (e.g., Fig 1c). We can then estimate parameter b_{ij}, which is the proportion of microsites that species *i* occupies when competing with species *j* for microsite occupancy (and vice versa for species *j*). While b_i equates to the area of fundamental niche space available to species *i* in a plot, b_{ij} equates to the area of species *i*'s realised niche space when seeds of species *j* are present at saturating density.

Using the definitions described above, we can calculate niche overlap as the area of overlap in the fundamental niches of each species, given by:

$$o_{ij} = (b_i - b_{ij}) + (b_j - b_{ji}). \quad \text{Equation 2}$$

The parameter o_{ij} can be expressed as a proportion of the fundamental niche space of each species by dividing it by either b_i or b_j. Similarly, we can measure a species' competitive ability relative to a second species as the proportion of the shared niche space captured by that species. For species *i* this is:

$$(b_j - b_{ji}) / o_{ij} \quad \text{Equation 3}$$

(the amount of species *j*'s niche space captured by species *i* at saturation as a proportion of the amount of overlapping niche space).

The above calculations are easily interpretable when species' realised niches are smaller than their fundamental niches, as expected due to competition. However, in our field experiments some species had higher recruitment in the presence of other species, implying facilitative rather than competitive interactions. This resulted in some realised niches being larger than the fundamental niches, which made it difficult to interpret the measures of niche overlap and competitive ability described above. To accommodate this, we can instead calculate the ratio:

$$d_{ij} = (b_i - b_{ij}) / b_i \qquad \text{Equation 4}$$

which is the proportion of species *i*'s safe-sites captured by species *j* when seeds of both species are at saturation. Parameter *d* can be interpreted as a measure of the potential impact of one species on another when both species are at saturating seed densities, and allows for both competitive and facilitative interactions (see below).

Interpreting the parameter d

A value of $d_{ij} = 0$ would mean that species *j* has no impact on the recruitment of species *i*. This could arise because: 1) the two species fundamental niches do not overlap, such that they partition the niche space; or 2) the fundamental niche of species *j* overlaps with species *i*, but species *i* always outcompetes species *j* for safe-site occupancy. We can distinguish between these alternatives by calculating d_{ji}, the proportion of species *j*'s safe-sites captured by species *i*. If $d_{ij} = d_{ji} = 0$ (Fig. 2a) then neither species affects the other, implying complete niche differentiation. If $d_{ij} = 0$ and $d_{ji} = 1$ (Fig. 2b) then the niche of species *j* must overlap completely with that of species *i*, and species *i* always outcompetes species *j* for shared niche space.

Values of d_{ij} and/or d_{ji} between 0 and 1 imply some degree of niche overlap with one (or both) species having a competitive impact on the other without complete exclusion. This could arise if species have partially or completely overlapping niches, with each species a superior

competitor in some portion of the shared niche space (e.g. Fig. 2c, with the species with the largest *d* value having the greatest competitive impact), or if they have partially overlapping niches with one species always the superior competitor for shared niche space (e.g. Fig. 2d). It is worth noting that in a situation where species have overlapping niches and each species excludes the other in half of shared safe-sites (Fig. 2e), the method would be unable to determine whether the impact of each species on the other arises because they are each competitively superior in half of shared safe-sites, or because they are competitively equal and sites were won at random (i.e. neutrality; Hubbell, 2001). Finally, while values of *d* cannot exceed 1 they can fall below 0, which would indicate that recruitment of a species was facilitated by the presence of a second species at seed saturation (Fig. 2f). We calculated *d* values and used these to infer niche overlap and the resulting competitive impact of one species on another in our experiments.

Field experiments

To illustrate our approach, we carried out two seed addition experiments in grassland on the University of Canberra campus, Australian Capital Territory. The grassland site resulted from historical land clearing (formerly grassy-woodland) and was dominated by a mixture of native and introduced species. Before the start of the experiment, the area was grazed by kangaroos and mowed regularly.

Experiment 1

In the first experiment, we aimed to measure niche overlap and the relative competitive ability of three grass species along a gradient of soil moisture availability. One species, *Rytidosperma caespitosum*, is native to the Australian Capital Territory and is common on dry, shallow soils, while the other two species (*Dactylis glomerata* and *Phalaris aquatica*) are non-native pasture grasses commonly found in areas with higher soil moisture. We were interested in why these

species varied in abundance along the gradient: was it because they had different fundamental niches and partitioned safe-sites accordingly, or did their fundamental niches overlap such that any differences in their relative abundances were due to interspecific competition for shared safe-sites?

We carried out the first experiment during austral summer 2015/2016. The study site was on an east-facing slope that had generally shallow soils with a pronounced gradient in soil moisture availability (Appendix S1) associated with soil depth. We fenced the site to prevent mowing and kangaroo grazing. A pilot study revealed very low rates of recruitment when seeds were added to established vegetation. Therefore, to enable recruitment of our target species, we removed the resident vegetation before adding seed. We cleared vegetation by applying glyphosate weedkiller and removing dead material by raking, repeating this procedure several times in the weeks prior to seed addition to deplete the soil seedbank as much as possible. After seed addition, species that had not been experimentally added to plots were removed as they appeared through careful spot application of glyphosate until our experimental plants had established and weeding of non-target plants was no longer possible without damaging our experiment. Because our study site is very dry, with mostly shallow soils and frequent periods without rain during summer, we watered soils at the time of seed sowing and during dry weather. Watering ensured that seeds germinated and survived, and maintained the moisture gradient throughout the experiment. Without watering, soil across the whole site would have dried out completely during periods without rain. Watering ensured that moist sites retained some moisture, while dry sites became dry again soon after watering.

We added seeds of each of the three species in monoculture to 0.3 × 0.3 m plots at each of six densities: 25, 75, 150, 500, 1250 and 2500 (corresponding to 278, 833, 1,667, 5,555, 13,888 and 27,775 seeds per m^2, respectively). Seed densities were chosen to span a range up to a maximum we thought would saturate microsites with seeds, and each species × density

257 treatment was replicated 10 times. Adding seeds of each species at different densities in
258 monoculture and counting the resulting number of recruits allowed us to fit recruitment curves
259 using Equation 1 and estimate b_i and n_i for each species.

260 For each pairwise combination of species, we added 2500 seeds of both species to the same
261 plot (polyculture), with each pairwise combination replicated 20 times. The aim was to ensure
262 that all microsites in these plots were saturated with seeds of both species such that they would
263 compete for any shared safe-sites, allowing us to calculate b_{ij} and b_{ji} and hence d_{ij} and d_{ji}
264 (Equation 4). The monoculture and polyculture plots were randomly distributed within two
265 blocks that were arranged such that one block was located at the drier end of the moisture
266 gradient and the other at the wetter end (Appendix S1). Each block comprised 156 plots of 0.4
267 × 0.4 m (each 0.3 × 0.3 m seed addition plot with a 0.05 m buffer around the edge of each plot
268 so they were at least 0.1 m apart) arrayed in 26 columns and 6 rows, with a 0.5 m walkway
269 every second row. Within each block, each monoculture treatment was replicated five times,
270 and each polyculture treatment replicated ten times (with 36 plots per block left over and having
271 no seed addition).

272 We added seeds to plots in December 2015 and counted the number of recruits in each plot
273 four months later (April 2016) when all species were beginning to flower. In February 2016
274 we measured relative soil moisture at the centre of each plot using a handheld soil moisture
275 sensor (Delta-T Devices, ML3 Sensor). We timed this measurement to occur 24 hours after
276 rain to ensure the rainwater had enough time to enter the soil but before the soil had completely
277 dried out, which was common during periods of low rainfall.

278 *Experiment 2*

279 The second experiment involved three native species (*Bothriochloa macra*, *Chloris truncata*
280 and *Rytidosperma caespitosum*) that commonly co-occur in grasslands around our field site

(e.g. Driscoll, 2017). Our aim was to understand the roles of niche availability, niche overlap and competition in influencing the co-occurrence of these species in a relatively homogenous habitat, particularly the extent to which they partitioned microsites at a fine-scale.

We carried out the second experiment during austral summer 2016/2017. We selected an area close to our first experiment, but on flat ground with no obvious moisture gradient. As with the first experiment, we removed established vegetation before the start of the experiment through herbicide application and raking, fenced the plots, carried out spot applications of glyphosate to kill non-target species until experimental plants had established, and watered the plots regularly. We added seeds in monoculture at the following densities: 50, 250, 500, 750, 1250 and 2500 (corresponding to 556, 2778, 5555, 8333, 13,888 and 27,775 seeds per m^2, respectively), and seeds in two-species polycultures at the highest density (27,775 seeds per m^2 for both species). The monoculture seed densities differed slightly from Experiment 1 because we wanted to better measure recruitment at intermediate seed densities. We replicated each monoculture treatment 10 times and each polyculture treatment 20 times. Plots were arranged in ten blocks that were each 6.3 × 4.9 m in size (including space for walkways). Each block contained one of each monoculture treatment and two of each polyculture treatment (with six empty plots per block). There were a total of 72 plots per block (720 overall). We added seeds in December 2016, and counted the number of recruits four months later, which corresponded with the onset of flowering for all species.

Analysis

For each experiment, we fitted Equation 1 to data on the number of recruits recorded at each level of seed addition, for both the monoculture (all seed densities) and polyculture (high seed density only) plots. We modelled variation in the observed number of recruits, r_{ik} of species i in plot k, using a negative binomial distribution:

$r_{ik} \sim \text{NegBinom}(\mu_{ik}, \lambda_i)$

$$\mu_{ik} = b_{ik} n_i \left(1 - e^{s_{ik}/n_i}\right)$$

where μ_{ik} is the mean number of recruits of species i in plot k, and λ_i is a dispersion parameter that captures unexplained differences among plots in the number of recruits. Smaller values of λ_i indicate greater variability among plots in the number of recruits, implying there is some unexplained factor(s) causing spatial aggregation of safe-sites, such that some plots have more and others fewer safe-sites than expected.

The value for b_{ik} for each plot varied depending on whether species were sown in monoculture or polyculture, and therefore whether we were estimating b_i or b_{ij}, respectively. Specifically, we modelled b_{ik} as follows:

$$\text{logit}(b_{ik}) = \alpha_i + \gamma_{ij}$$

Where α_i is the estimate of b_i on the logit scale, and γ_{ij} is the difference between b_i and b_{ij} (on the logit scale), which was set to zero for monoculture plots and estimated from the data for polyculture plots. We used the resulting estimates to calculate d_{ij} and d_{ji} using Equation 4.

To examine how safe-site availability varied along the moisture gradient in Experiment 1, we included an additional term in the model for each species:

$$\text{logit}(b_{ik}) = \alpha_i + \gamma_{ij} + \beta_i * \text{moisture}_k$$

where moisture_k is the measure of soil moisture for plot k (centred on the mean) and β_i is a species-specific parameter estimated from the data that describes how safe-site availability changes with soil moisture (on the logit scale).

We fitted models and did the resulting calculations in a Bayesian framework using the software JAGS v4.2.0 (Plummer, 2003), which we ran using the package jagsUI (Kellner, 2015) in R

v3.4.2 (R Development Core Team, 2017). The parameters describing the proportion of safe-sites (α_i, γ_{ij} and β_i) were constrained to reasonable values on the logit scale by specifying a Cauchy prior distribution with a median of 0 and scale of 2.5, following Gelman (2008). For each species, the parameter n_i was given a weakly informative prior, specified as coming from a normal distribution with mean 1000 and large variance, and the dispersion parameter λ_i was given a broad uniform prior (0-500). We used median values of the posterior distributions of all parameters to characterize central tendency and 95% credible intervals to capture uncertainty in our parameter estimates.

RESULTS

Experiment 1

When seeds of each species were sown at varying densities in monoculture, the recruitment curves fitted using Equation 1 all approached an asymptote at high seed densities (Fig. 3). The estimated asymptotic number of recruits is the estimated number of safe-sites per plot ($b_i n_i$; a measure of fundamental niche availability). That all species approached an asymptote implies that seed supply exceeded the number of safe-sites available for recruitment, such that seeds competed for safe-site occupancy at high seed densities. The number of safe-sites per plot was greatest for the native *R. caespitosum* (18.9, 95% credible intervals 10.6 – 39.1) and lower for the non-native species, *P. aquatica* (9.4, 95% credible intervals 3.8 – 27.1) and *D. glomerata* (8.2, 95% credible intervals 3.6 – 19.6).

Values of n_i (the number of microsites that could theoretically support one individual) were similar for all three species (Fig. 4a). However, *R. caespitosum* had more safe-sites per plot (more fundamental niche space) because a greater proportion of microsites were suitable for its recruitment (b_i, Fig. 4b). Approximately 2% of microsites were safe for *R. caespitosum* compared to less than 1% for *D. glomerata* and *P. aquatica*. The dispersion parameters (λ_i)

revealed more spatially variable recruitment for *D. glomerata* and *P. aquatica* relative to *R. caespitosum* (0.95 for *R. caespitosum* versus 0.40 and 0.14 for *D. glomerata* and *P. aquatica*, respectively, with lower values indicating greater spatial aggregation of safe-sites; Fig. 4c).

The finding that, for *R. caespitosum*, there were more safe-sites per plot and recruitment was less variable among plots appeared due to its tolerance of a wider range of soil moisture conditions relative to the two non-native species. While *R. caespitosum* had a relatively even rate of recruitment across the moisture gradient, the two non-native species had low rates of recruitment at low soil moisture with increasing recruitment at higher soil moisture, particularly *P. aquatica* (Fig. 5).

When seeds were at saturation, the presence of a second species in the polyculture plots did not substantially alter the number of recruits relative to the monoculture plots for any species (Fig. 3). For all pairwise combinations, estimates of d_{ij} and d_{ji} had values close to zero, albeit with wide 95% credible intervals (Fig. 4d-f). As such, there was no clear evidence that the fundamental niches of the three study species overlapped and that they competed for safe-site occupancy.

Experiment 2

In Experiment 2, recruitment curves for all species again reached an asymptote at high seed densities, indicating that safe-sites rather than seed supply limited further recruitment (Fig. 6). In monoculture plots, *R. caespitosum* had the lowest asymptotic number of recruits, with an estimated 0.8 individuals recruiting at seed saturation (95% credible intervals 0.4 – 1.4), compared with 3.3 individuals (95% credible intervals 2.2 – 4.9) for *B. macra* and 3.5 individuals (95% credible intervals 2.8 – 4.9) for *C. truncata*.

373 Differences in the number of safe-sites per plot for each species ($b_i n_i$) resulted from both
374 differences in the total number of microsites available (n_i; Fig. 7a) and the proportion of
375 microsites that were safe for recruitment (b_i; Fig. 7b). The estimated number of microsites per
376 plot was around five times higher for *B. macra* and *R. caespitosum* than for *C. truncata* (around
377 1000 compared to just over 200) suggesting that, after four months, the area required to support
378 a single *C. truncata* individual was greater than for the other two species. In contrast, the
379 proportion of microsites that were safe-sites was higher for *C. truncata* (around 1.5%) than *B.*
380 *macra* (less than 0.01%) and *R. caespitosum* (less than 0.001%), suggesting greater niche
381 availability for *C. truncata*. The dispersion parameter (λ_i; Fig. 7c) indicated high spatial
382 variation in safe-site availability for *B. macra* and *R. caespitosum* among plots (λ_i = 2.4 and
383 3.4, respectively), and a more even distribution of safe-sites among plots for *C. truncata* (λ_i =
384 271.7).

385 Neither the recruitment of *B. macra* (Fig. 6a) nor *R. caespitosum* (Fig. 6c) declined when seeds
386 of these species were added in polyculture relative to monoculture plots. Values of *d* for both
387 species (Fig. 7d) were close to zero, suggesting these species occupied distinct niches and did
388 not compete for safe-site occupancy. In contrast, recruitment of *B. macra* declined when seeds
389 were added together with those of *C. truncata* (Fig. 6a) but there was no concurrent decrease
390 in recruitment of *C. truncata* (Fig. 6b). Values of *d* indicated the two species had overlapping
391 niches, with *C. truncata* the superior competitor for shared niche space: *C. truncata* occupied
392 around 45% of microsites that would otherwise have been safe-sites for *B. macra*. There was
393 evidence that *B. macra* facilitated *C. truncata* such that recruitment of *C. truncata* increased in
394 plots where *B. macra* was present (Fig. 6c). A *d* value for *B. macra* of -0.43 (Fig., 7e) suggests
395 a 43% increase in the number of safe-sites (and hence niche space) available to *C. truncata*,
396 albeit with wide credible intervals.

The recruitment of *R. caespitosum* also declined when added together with seeds of *C. truncata*, with no concurrent decline in *C. truncata* recruitment. Values of *d* again suggest this was due to niche overlap with *C. truncata* the superior competitor for shared niche space. In polyculture, *Chloris truncata* occupied more than 80% of safe-sites that *R. caespitosum* could otherwise have occupied (Fig. 7f), with some indication of facilitation of *C. truncata* by *R. caespitosum* (value of *d* less than 1), though credible intervals were wide and overlapped zero.

DISCUSSION

Testing ideas about how niche and competitive processes determine the distribution and abundance of species is challenged by the lack of a single framework to empirically quantify niche availability, niche overlap and competitive ability in the field. Niche availability is particularly difficult to measure since most approaches rely on identifying the specific resource or environmental factors that limit species performance, and these factors can vary at quite fine spatial scales (Silvertown, Dodd, Gowing, & Mountford, 1999; Vivian-Smith, 1997). We have addressed this challenge by developing a model that conceptualizes the niche in terms of microsites that are safe for seedling recruitment. We applied our model to two field experiments to show how this allows us to: 1) quantify variation in species fundamental niche availability; and 2) estimate the degree to which two species fundamental niches overlap and their relative competitive ability in competition for shared niche space. One advantage of our approach is that it can be applied without knowing the specific niche axes controlling species distributions.

Niche partitioning along environmental gradients

Experiment 1 shows how our approach can help identify the relative importance of niche partitioning and competition for shared niche space in explaining species distributions along known environmental gradients (Chase, 2007; Chesson, 1994; Kneitel & Chase, 2004) or among habitats (Harrison, Cornell, & Moore, 2010). Our results were consistent with strong

niche partitioning ($d_{ij} = d_{ji} = 0$ for pairwise combinations of all three species), suggesting that variation in recruitment along the gradient likely reflects species independent responses to moisture availability rather than being the outcome of competitive interactions. Relative to the two non-native species, the native species *R. caespitosum* had a wider fundamental niche in the sense of having generally higher and more even recruitment along the moisture gradient (Fig. 5), with higher values of the dispersion parameter indicating less among-plot variation in recruitment. The two non-native species had low recruitment at low soil moisture with safe-site availability being more patchy (low values of the dispersion parameter, λ) and concentrated in areas with high soil moisture availability. Despite both non-native species preferring sites with higher moisture, there was no evidence that they competed for safe-site occupancy. Rather, they appeared to partition safe-sites within plots.

Niche and competitive differentiation along unidentified axes

With no obvious environmental gradient, the results from Experiment 2 demonstrate how quantifying safe-site availability can reveal how species partition or compete for niche space in the absence of any clearly defined niche axes (Harper et al., 1965). The fundamental niche of *C. truncata* overlapped with both *B. macra* and *R. caespitosum*, with *C. truncata* being the dominant competitor, while *B. macra* and *R. caespitosum* showed niche differentiation.

The faster growth and larger size of *C. truncata* individuals likely explains their competitive superiority and this, coupled with high niche availability, explains why they dominated cover in plots (Appendix S2). *Chloris truncata* had a high value for *b* and a low value for the dispersion parameter λ, suggesting that a large proportion of microsites were safe and these were relatively evenly distributed across plots. Conversely, a low value for *n* indicated fewer microsites per plot for *C. truncata* relative to other species, implying *C. truncata* individuals took up more space at four months of age. This was consistent with observations of species growth rates (Appendix S2): at low density, as few as five individuals of *C. truncata* could

446 achieve 100% vegetation cover in a plot, while the same number of *B. macra* reached a
447 maximum cover of only around 50% and *R. caespitosum* never recruited as many as five
448 individuals in a plot, attaining a maximum cover of 10%.

449 *Fine-scale niche partitioning*

450 Our results highlight the fine-scales over which microsite conditions can vary to allow species
451 to co-occur. This was particularly evident in Experiment 2. Although *C. truncata* had a large
452 competitive impact on both *B. macra* and *R. caespitosum*, leading to their competitive
453 exclusion at the microsite level, niche differentiation at the plot level allowed both species to
454 persist even when *C. truncata* was present. Indeed, around half of the safe-sites for *B. macra*
455 remained safe when *C. truncata* seeds were present at saturating density. Thus, although
456 competitive exclusion can occur at the microsite scale, differences among microsites results in
457 opportunities for niche differentiation and potentially neutral processes to occur within small,
458 apparently homogenous plots. This highlights a role of competitive refugia in allowing species
459 persistence at fine-scales as well as across environmental gradients (Pickett & Bazzaz, 1978).
460 Moreover, the sensitivity of species to fine-scale variation in microsite conditions could explain
461 how species can partition niches to locally co-occur within apparently homogenous
462 environments (Blonder et al., 2018; Harper et al., 1965; Vivian-Smith, 1997), and why some
463 studies have failed to detect competitive exclusion in systems with no obvious axes of niche
464 differentiation (Silvertown, 2004).

465 *Facilitation*

466 Facilitation can be as important as competition in shaping species distributions (Callaway &
467 Walker, 1997). There was strong evidence for facilitation in Experiment 2 with *C. truncata*
468 having higher recruitment in the presence of other species, especially *B. macra*. Facilitation is
469 often associated with stressful environments where the presence of one species can benefit

others by providing shelter or enabling resource uptake (Bertness & Callaway, 1994). Although it was not clear what the mechanism for facilitation in Experiment 2 might be, the results are consistent with a situation in which *C. truncata* outcompeted *B. macra* for occupancy of shared safe-sites where their fundamental niches overlapped, but the presence of *B. macra* increased the number of safe-sites for *C. truncata* and led to a larger realised than fundamental niche in places where the two species otherwise occupied distinct niches.

Although our findings in Experiment 1 suggest little overlap in species fundamental niches, resulting in niche differentiation, the credible intervals associated with the *d* parameter were wide. Thus, it is possible that a more complex outcome, involving shifts in the relative importance of competition and facilitation along the moisture gradient, may have occurred, as has previously been demonstrated for species interactions along moisture gradients (Eckstein, 2005). Detecting such shifts would require greater experimental replication to untangle how niche availability and competitive outcomes varied at points along the gradient.

Beyond recruitment

Our approach focuses on recruitment as an important determinant of species presence and abundance in a community (Chu & Adler, 2015; Grubb, 1977). Nonetheless, niche requirements and competitive interactions among species can change across life-stages (Freckleton, Watkinson, & Rees, 2009; Grubb, 1977). Consequently, patterns that emerge from experiments focused on early recruitment may not reflect the range of potential outcomes as individuals age. Adults generally have broader fundamental niches and are more tolerant of competition than seedlings, while perennial plant species may gain a competitive advantage as they grow by pre-empting space that would otherwise be lost to a competitor (Corbin & D'Antonio, 2004; Seabloom et al., 2013). Our approach makes no predictions as to how patterns of niche versus competitive differentiation during recruitment might translate to long-

494 term demographic outcomes in successive generations. Nevertheless, tracking changes in the
495 model parameters through time can provide insight into how niche availability and competitive
496 interactions change as individuals age (Duncan et al., 2009; Miller et al., 2014), meaning our
497 method could yield insights into aspects other than the recruitment niche. Integrating model
498 parameters at different life-stages into demographic models is a potential avenue for future
499 research, and would help place some of the findings revealed by our method in a wider context
500 to understand their longer-term implications.

501 *Conclusions*

502 We have used two field experiments to demonstrate how the parameters obtained from a
503 recruitment model can be interpreted in terms of niche availability, niche overlap and
504 competitive ability, and explored general patterns that emerge from this. Our experiments
505 highlight the potential for fine-scale niche differentiation to allow multiple species to locally
506 co-occur. While this is a well-known mechanism to explain species coexistence (Stowe &
507 Wade, 1979), our approach provides a way to quantify the degree to which species partition or
508 compete for niche space at fine-scales without *a priori* knowledge of their specific niche
509 requirements. In this way, our approach is a step towards understanding the processes that
510 determine species distribution and abundance using relatively straightforward experiments.
511 Applying our approach to known gradients, as in the soil moisture experiment, has the potential
512 to address hypotheses about how processes such as niche partitioning and relative competitive
513 ability change along gradients to influence species distributions. Together, these approaches
514 suggest the method has wide applicability in resolving some important questions in plant
515 ecology.

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Author contributions:

JAC and RPD conceived the idea. EMW, JAC and RPD designed the study. EMW and RPD carried out the field work and analysed the data. EMW wrote the first version of the manuscript and all authors edited the manuscript.

Data accessibility: Data and code available from the Dryad Digital Repository: doi:10.5061/dryad.sm76ms5.

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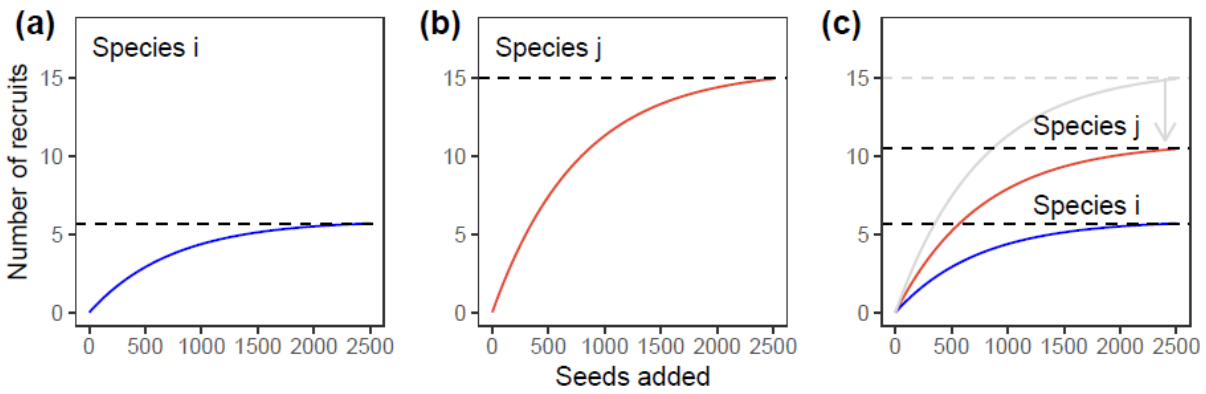
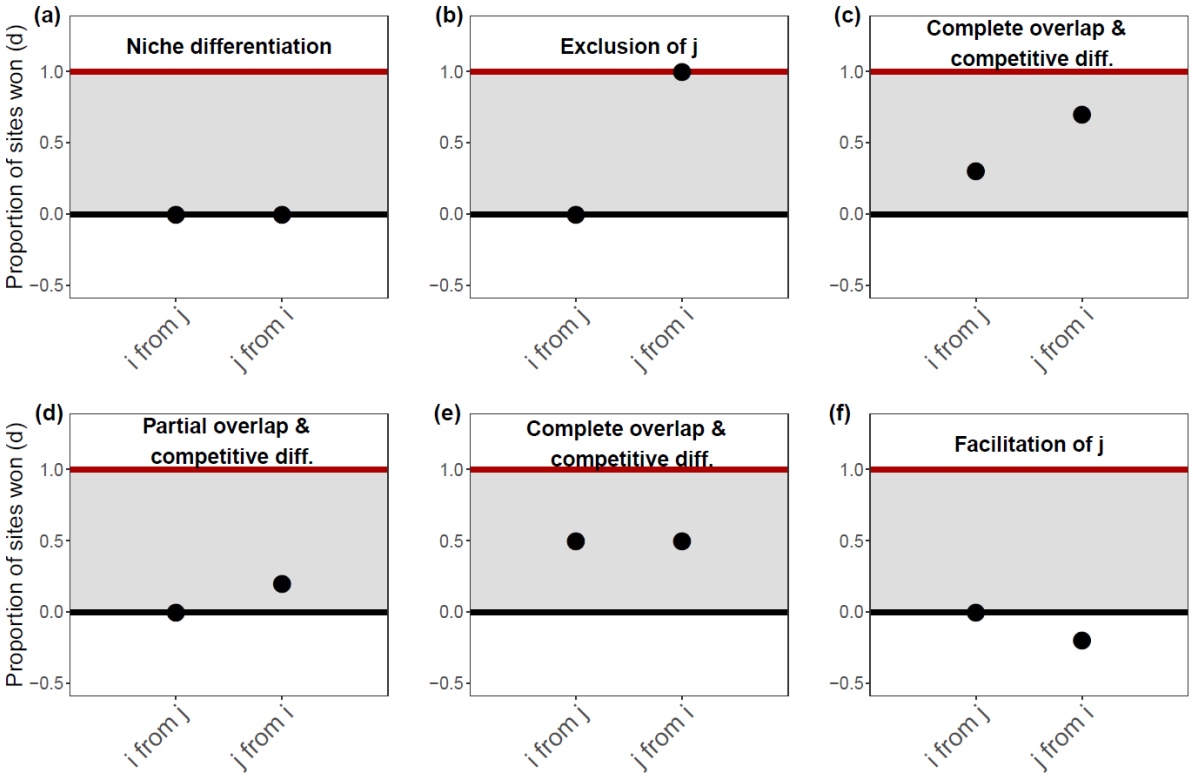


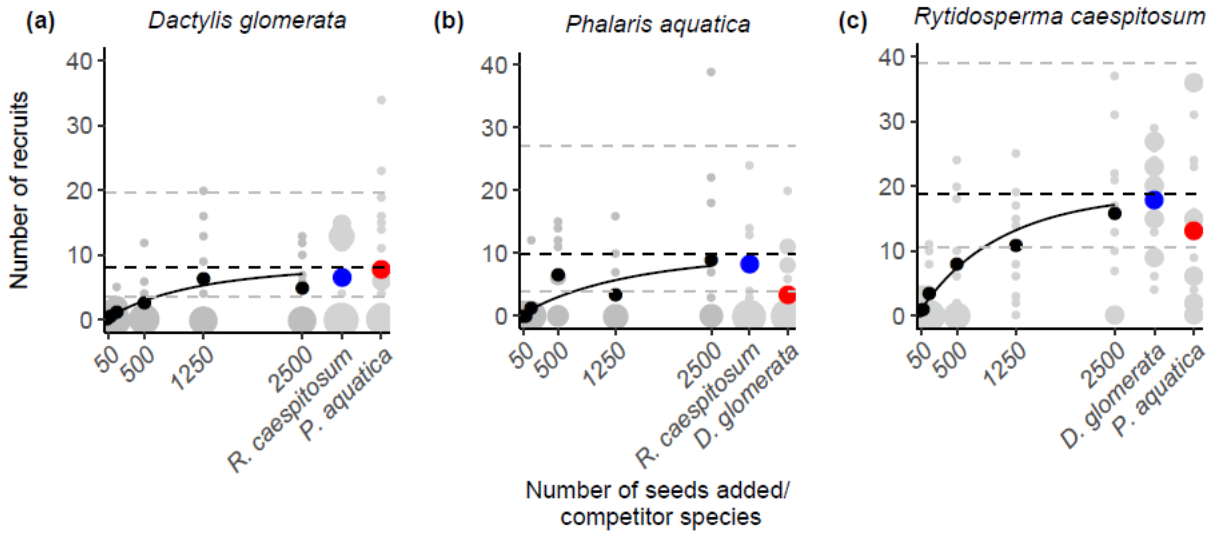
666

667 **Figure 1. Conceptual diagram illustrating how recruitment curves can be used to estimate**
668 **niche availability for two species, *i* and *j*, in monoculture (fundamental niche; a, b) and**
669 **polyculture (realised niche; c)**. When seeds of (a) species *i* or (b) species *j* are added at varying
670 densities to plots in monoculture, Equation 1 can be fitted to data on the resulting number of
671 recruits to estimate parameters b_i and n_i, and b_j and n_j, giving a relative measure of niche
672 availability for each species: $b_i n_i$ (dashed line in a) and $b_j n_j$ (dashed line in b). c) Adding seeds
673 of species *i* and *j* to plots in polyculture at saturating seed densities then allows estimation of
674 b_{ij} and b_{ji}, which is the proportion of microsites that are safe for species *i* in polyculture with
675 species *j*, and the proportion of microsites that are safe for species *j* in polyculture with species
676 *i*, respectively. Here, the addition of seeds of both species in polyculture lowers the recruitment
677 of species *j* (red curve; $b_{ji} n_j$ is lower than $b_j n_i$), but does not affect recruitment of species *i* (blue
678 curve; $b_{ij} n_i$, is equal to $b_i n_i$).

679

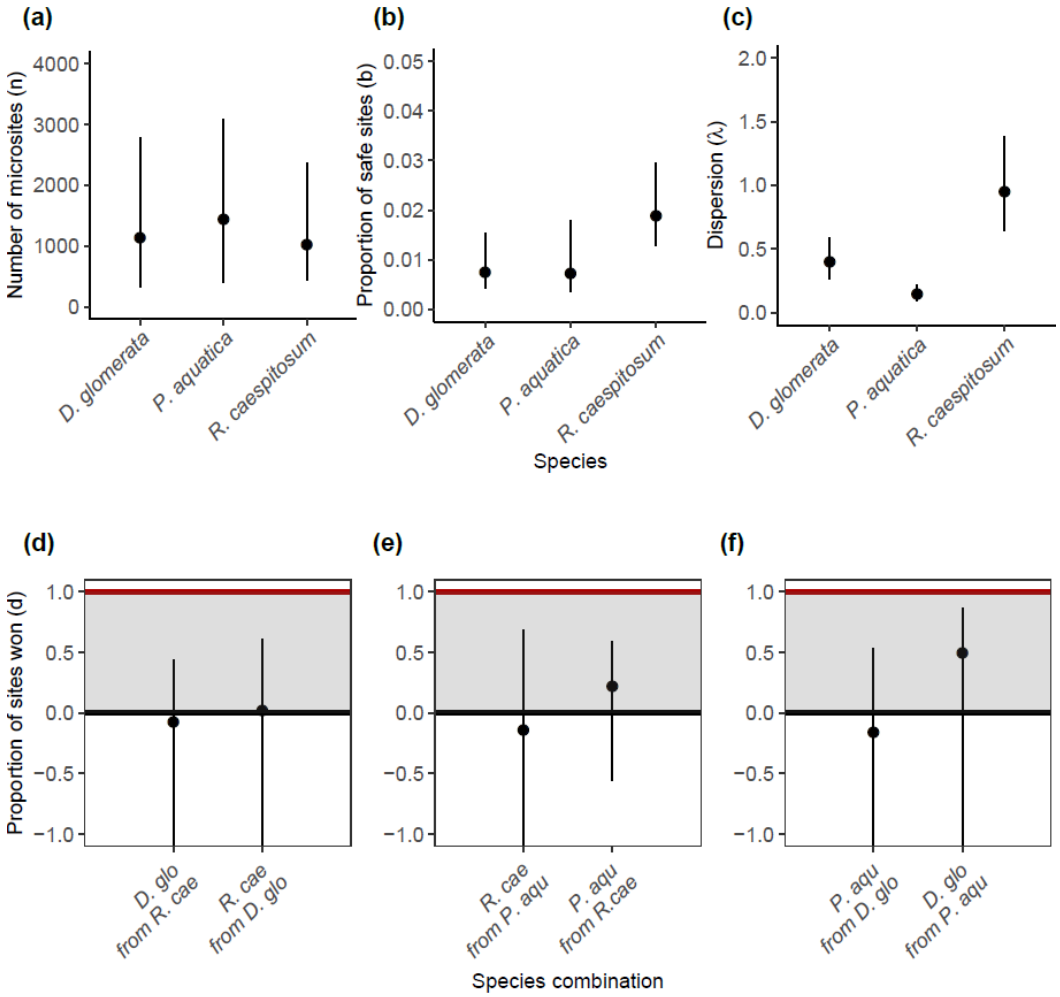


680 **Figure 2. Interpreting the parameter *d*.** The parameter *d* describes the proportion of safe-
681 sites won by one species from the other, with d_{ji} the proportion of safe-sites won from species
682 *j* by species *i*, and d_{ij} the proportion of safe-sites won from species *i* by species *j*. a) Two species
683 are completely differentiated with regard to their safe-site requirements (complete niche
684 differentiation) where $d_{ij} = d_{ji} = 0$; b) In contrast, where $d_{ji} = 1$, species *j* is competitively
685 excluded by species *i*: species *i* shares all of species *j*'s safe-sites and outcompetes species *j* for
686 occupation of those safe sites. Various outcomes between these two extremes are possible
687 depending on the degree of niche overlap and species relative competitive abilities (e.g. c-e),
688 including situations (e) where species have identical niches and are either competitively equal
689 (neutral outcome), or are each a superior competitor in half of shared niche space. Facilitation
690 of one species by another (an increase in the proportion of microsites that are safe) is also
691 possible (f). Red line indicates complete competitive exclusion of one species by another,
692 points in the grey shaded plot area indicate niche overlap, points in the white plot area indicate
693 facilitation.



694

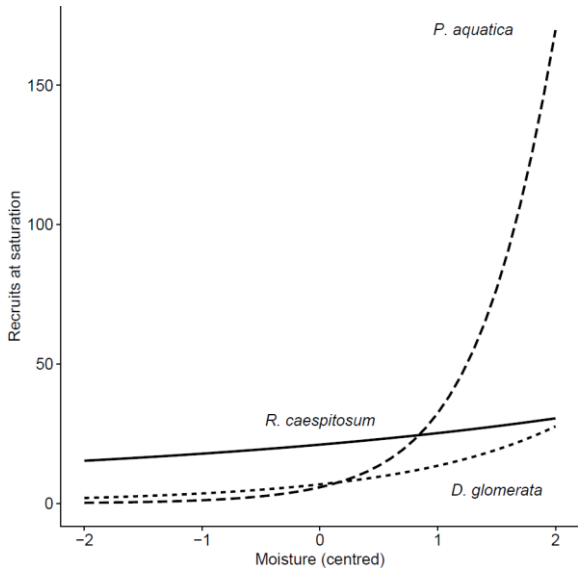
695 **Figure 3. Fitted recruitment curves (black solid lines) for two exotic and one native species**
696 **across a known moisture gradient in Experiment 1.** Dashed horizontal lines show the
697 number of safe-sites at seed saturation (i.e. $b_i n_i$: niche availability) for each species when sown
698 in monoculture (black line shows the median and grey lines the 95% credible intervals); black
699 points show the mean number of recruits per plot at each seed density; grey points show the
700 raw data for the number of recruits per plot, with size proportional to the number of plots
701 represented; coloured points show the mean recruitment per plot in polyculture (competitor
702 species on the x axis; blue points indicate a native competitor and red an exotic).



703

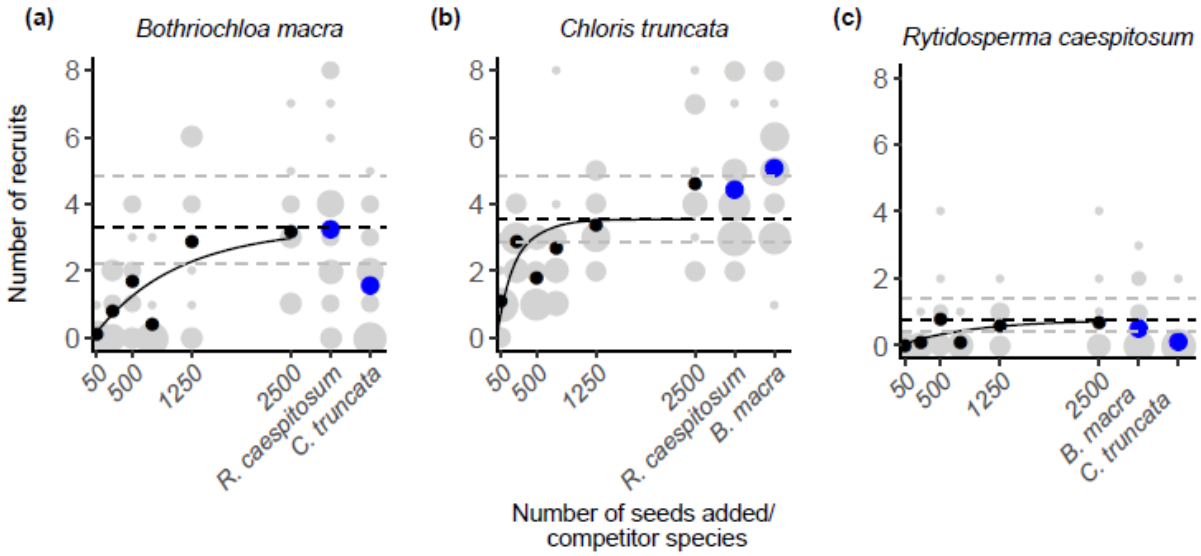
704 **Figure 4. Model parameters for the two exotic and one native species in Experiment 1.**
705 The parameters from the recruitment function describe: a) the median number of microsites per
706 plot for each species; b) the proportion of microsites that are safe; and c) the dispersion of safe
707 sites through space for each species when sown in monoculture. d-f) Values of d_{ij} and d_{ji} (the
708 proportion of safe sites won by one species from another) for each species in each pairwise
709 combination. Species codes in d-f: R. cae = *Rytidosperma caespitosum*; D. glo = *Dactylis*
710 *glomerata*; P. aqu = *Phalaris aquatica*. Red line indicates complete competitive exclusion of
711 one species by another, points in the grey shaded plot area indicate niche overlap, points in the
712 white plot area indicate facilitation. Bars represent 95% credible intervals.

713



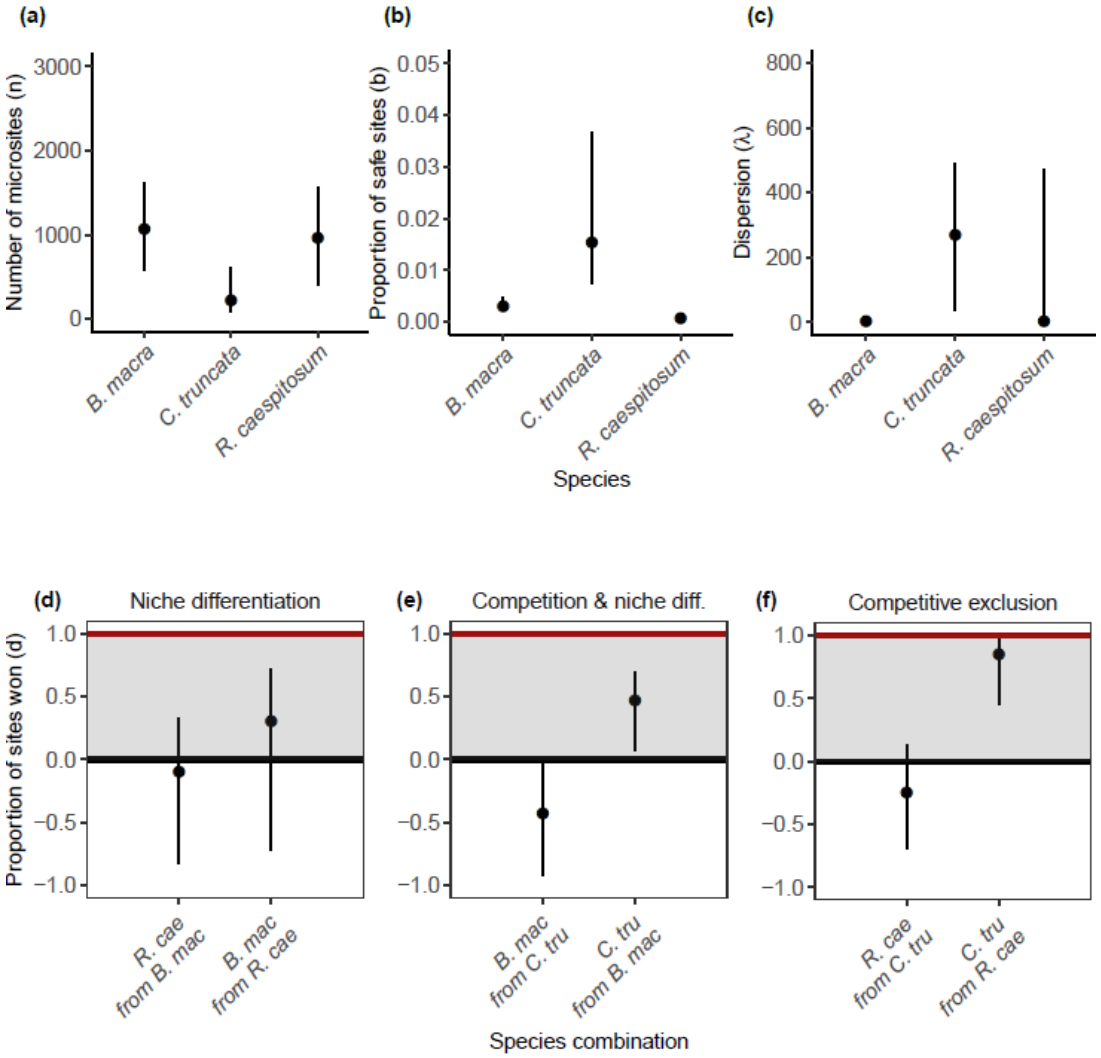
714

715 **Figure 5. Modelled estimates of the mean number of recruits predicted for each species**
716 **when all safe-sites are saturated across the soil moisture gradient in Experiment 1.** Soil
717 moisture values have been centred and standardised to mean = 0 and standard deviation = 1.



718

719 **Figure 6. Fitted recruitment curves (black solid lines) for the three native species in**
720 **Experiment 2**. Dashed horizontal lines show the number of safe-sites at seed saturation (i.e.
721 $b_i n_i$: niche availability) for each species when sown in monoculture (black line shows the
722 median and grey lines the 95% credible intervals); black points show the mean number of
723 recruits per plot at each seed density; grey points show the raw data for the number of recruits
724 per plot, with size proportional to the number of plots represented; coloured points show the
725 mean recruitment per plot in polyculture (competitor species on the x axis).



726 **Figure 7. Model parameters for the three native species in Experiment 2.** The parameters
727 from the recruitment function describe: a) the median number of microsites per plot for each
728 species; b) the proportion of microsites that are safe; and c) the dispersion of safe sites through
729 space for each species when sown in monoculture. d-f) Values of d_{ij} and d_{ji} (the proportion of
730 safe sites won by one species from another) for each species in each pairwise combination.
731 Species codes in d-f: B. mac = *Bothriochloa macra*; C. tru = *Chloris truncata*; R. cae =
732 *Rytidospermum caespitosum*. Red line indicates complete competitive exclusion of one species
733 by another, points in the grey shaded plot area indicate niche overlap, points in the white plot
734 area indicate facilitation. Bars represent 95% credible intervals.